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An Early Miocene bumble bee from northern Bohemia (Hymenoptera, Apidae)

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Abstract

A new species of fossil bumble bee (Apinae: Bombini) is described and figured from Early Miocene (Burdigalian) deposits of the Most Basin at the Bílina Mine, Czech Republic. *Bombus trophonius* **sp. n.**, is placed within the subgenus *Cullumanobombus* Vogt and distinguished from the several species groups therein. The species is apparently most similar to the Nearctic *B.* (*Cullumanobombus*) *rufocinctus* Cresson, the earliest-diverging species within the clade and the two may be related only by symplesiomorphies. The age of the fossil is in rough accordance with divergence estimations for *Cullumanobombus*.

Keywords

Anthophila, Apoidea, *Bombus*, Burdigalian, geometric morphometrics, Neogene

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Introduction

Bumble bees (Bombini: *Bombus* Latreille) are among the most recognized and studied of all bees, second only to the honey bees (Apini: *Apis* Linnaeus) and perhaps tied with the stingless bees (Meliponini). These robust, densely setose, and variably colored species are mainly found in colder temperate regions (Rasmont et al. 2015), and are distributed throughout the Americas, across the Palearctic and Oriental Regions, but are characteristically absent from Africa and Australia (Michener 2007). Together with the orchid bees (Euglossini) and the aforementioned Apini and Meliponini, bumble bees represent one of the four surviving tribal lineages of the corbiculate Apinae (Engel 2001a, Michener 2007). Varied extinct lineages representing stem groups or breaking the otherwise long branches between our modern corbiculates have been discovered from the Paleogene (Cockerell 1908, Engel 1998a, 2001a, Wappler and Engel 2003, Patiny et al. 2007, Engel et al. 2013, 2014), and some of these reveal that the bombine habitus is overall generalized and plesiomorphic for the Corbiculata (*e.g.*, Engel 2001a). These extinct clades are also the fossils for which the most information has been accumulated regarding their pollen-collecting behaviors (Wappler et al. 2015, Grímsson et al. 2017). While controversy remains regarding their relationship to either Meliponini or Meliponini + Apini (*e.g.*, Michener 1990, Schultz et al. 1999, 2001, Engel 2000a, 2001b, Noll 2002, Cardinal and Packer 2007, Kawakita et al. 2008, Kwang et al. 2017), the 263 extant species of Bombini are likely a comparatively young, monophyletic crown group at the apex of an otherwise older lineage diverging from a common ancestor with meliponines and apines sometime in the latest Cretaceous (Engel 2000, 2001a), leaving a ghost record of stem groups between this divergence and perhaps the Early to mid-Eocene. It is possible that the origin of the crown group for bumble bees could have been associated with a global cooling event that occurred during the mid-Eocene (Hansen et al. 2013, Pound and Salzmann 2017). In fact, this same pattern seems to be true also for euglossines (crown group perhaps of Eocene-Oligocene age) and perhaps apines (latest Eocene or earliest Oligocene age), while crown-group meliponines extend back to the Maastrichtian (Michener and Grimaldi 1988, Engel 2000b). In general, the geological history of the corbiculate bees encompasses one of the more extensive records of fossils among the Apoidea (Michez et al. 2012), with diverse representatives spanning the Cenozoic for the highly eusocial Apini (Engel 1998b, 1999a, 2006, unpubl. data, Engel et al. 2009, Kotthoff et al. 2011, 2013) and Meliponini (Michener 1982, Camargo et al. 2000, Engel 2001a, unpubl. data, Greco et al. 2011, Engel and Michener 2013a, 2013b). Fossils of the communal or solitary Euglossini (Engel 1999b, 2014, Hinojosa-Díaz and Engel 2007) and the primitively eusocial Bombini (Michez et al. 2012, Wappler et al. 2012) are less common, and for this reason are of greater interest when new material becomes available. It is in this context that we provide here a descriptive account for a fossil *Bombus* from the Early Miocene of northern Bohemia (Fig. 1), representing an early record of the subgenus *Cullumanobombus* Vogt. We provide this description here so that the species' name might be available for use in a forthcoming work on the general review of fossil record of Bombini (Dehon et al. in prep.).

Material and methods

Geological setting. The Early Miocene coal seam overlaying deposits of the Most Basin at Bílina Mine represents one of the classic paleontological localities in northern Bohemia, studied intensively since the 19th century. The depositional environment and stratigraphy of the upper coal seam deposits at Bílina Mine have been summarized by Kvaček et al. (2004) and updated by Pešek et al. (2014), while the age of the primary insect-bearing layers within the Holešice Member corresponds to the early Burdigalian, from 18–20 Ma (Shrbený et al. 1994, Rajchl et al. 2009). The locality at the time was characterized by a subtropical/warm temperate and temperate climate (Kvaček et al. 2004). The insect fauna at Bílina Mine includes more than 350 specimens of terrestrial and aquatic groups assigned to 31 families in 11 orders (*e.g.*, Prokop and Nel 2000, Prokop 2003, Fikáček et al. 2008), with specimens of Hymenoptera, particularly ants, being most prevalent (Prokop and Nel 2003, Wappler et al. 2014). In addition, the overlaying deposits at Bílina Mine have been studied intensively for their remarkably well-preserved record of plant-arthropod interactions (*e.g.*, Prokop et al. 2010, Knor et al. 2012, 2013). The bumble bee described here is preserved in a fine clay overlaying the coal seam, and has become carbonized, thus the chitinous integument is modified by the process of fossilization (Figs 1–3).

Specimen repository and descriptive terminology. The fossil reported herein was retrieved from the collection of Zdeněk Dvořák, deposited in the museum holdings of the Bílina Mine Enterprises in Bílina, Czech Republic. The specimen was examined dry using a Nikon SMZ 645 stereomicroscope. Photographs were taken using a Canon EOS 550D digital camera coupled to a MP-E 65 mm macro lens. The description is provided here in the aim of improving diagnostic and species-level accounts of living and fossil bees (*e.g.*, Engel 2011, Gonzalez et al. 2013). Morphological terminology follows that of Engel (2001a) and Michener (2007), with the format for the descriptions augmented from those of Wappler et al. (2012) and Dehon et al. (2014).

Geometric morphometric analyses of forewing shape. Prior to description using traditional venational traits, the present fossil was analyzed for its placement among other *Bombus* based on a geometric morphometric analysis of wing shape using vein landmarks. This method has proved useful in placing otherwise difficult to treat fossil species (*e.g.*, Kotthoff et al. 2011, 2013, Dewulf et al. 2014, Dehon et al. 2017), including fossil bombines (Wappler et al. 2012, Dehon et al. in prep.). Geometric morphometric analysis (Pavlinov 2001) of insect wings is a valuable tool given that it is easily implemented, comparatively inexpensive, and the wings themselves are comparatively rigid, two-dimensional structures, species specific, and frequently well preserved in fossil specimens, albeit at times taphonomically distorted. Furthermore, forewing veins and their intersections are homologous among bees with three submarginal cells, like bumble bees (Ross 1936, Michener 2007). The method is rather robust at diagnosing and discriminating taxa at different levels (*e.g.*, Pretorius 2005, Petit et al. 2006, Sadeghi et al. 2009, Francoy et al. 2012, Perrard et al. 2014), and has been employed successfully in palaeontological studies for evaluating the taxonomic affini-

ties of otherwise difficult to determine fossils (*e.g.*, Kennedy et al. 2009, Michez et al. 2009, Dehon et al. 2014, 2017, Dewulf et al. 2014, Perrard et al. 2016). Moreover, several studies have demonstrated the application of forewing shape analyses for discriminating subgenera, species, and populations of bumble bees (*e.g.*, Aytekin et al. 2007, Wappler et al. 2012, Barkan and Aytekin 2013).

Morphometric analyses followed the procedures as outlined by Wappler et al. (2012) and Dehon et al. (2017, in prep.). As in Dehon et al. (2017), we employed three datasets to assess the taxonomic affinities of the fossil at different taxonomic levels by sampling broadly across extant and extinct tribes with the same number of submarginal cells as bumble bees. The first dataset consisted of a comprehensive sampling of bee tribes in order to maximize the shape diversity of our analyses, and this dataset was previously tested by Dehon et al. (2017). The dataset includes 20 specimens and four species per tribe, and whenever possible five specimens per species, and ultimately represented 979 female specimens from seven families, 18 subfamilies, 50 tribes, 135 genera, and 226 species. This first dataset was used to estimate the similarity of the fossil relative to the tribe Bombini (Suppl. material 1), and to determine a group of five tribes (i.e., Ancylaini, Tarsaliini, Emphorini, Euglossini, and Tetrapediini) exhibiting an overall similar wing shape to bumble bees. A second dataset sampled species more extensively across the tribe Bombini and the aforementioned four tribes with similar wing shapes. This was done in order to extend the shape diversity inside the target group. This dataset sampled 15 subgenera and 210 species of bumble bees, accounting for a total of 841 specimens, each species represented by a maximum of five specimens (Suppl. material 2). The dataset represented 100% of the subgeneric diversity and more than 80% of the world's species. In addition, this second dataset included additional Ancylaini and Tarsaliini (two genera, nine species, and 25 specimens), Emphorini (four genera, 12 species, and 28 specimens), Euglossini (five genera, 11 species, and 55 specimens), and Tetrapediini (two genera, seven species, and 26 specimens) in the second dataset. Lastly, after confirmation of the affinities of the fossil with contemporary Bombini based on the second dataset, we considered a third dataset restricted entirely to bumble bee specimens so as to better assess the affinities of the fossil among modern subgenera of *Bombus* (*i.e.*, the dataset from Suppl. material 2 with all groups except Bombini excluded).

For the reference datasets, left forewings were photographed using an Olympus SZH10 microscope combined with a Nikon D200 camera. Photographs were input in the software tps-UTIL 1.69 (Rohlf 2013a). The forewing shape was then captured by digitizing two-dimensional Cartesian coordinates of 18 landmarks on the wing venation and cells (refer to diagram of landmarks presented in Dehon et al., 2017: their figure 1), with the software tps-DIG version 2.27 (Rohlf 2013b). The configurations of the landmarks were superimposed using the GLS Procrustes superimposition in R version 3.0.2 (Rohlf and Slice 1990, Bookstein 1991, Adams and Otárola-Castillo 2013, R Development Core Team 2013). The closeness of the tangent space to the curved shape space was assessed using the software tps-SMALL v1.25 (Rohlf 2013c) by calculating the least-squares regression slope and the correlation coefficient between the Euclidean distances in the tangent space with the Procrustes distances in the shape

space (Rohlf 1999). Prior to assignment of the Bílina fossil, discrimination of the wing shapes of the various taxa was assessed by Linear Discriminant Analyses (LDA) of the projected aligned landmark configurations. We did a LDA with the second dataset (*i.e.*, bumblebees + five similar tribes), with tribe level as *a priori* groupings (Suppl. material 3) (a similar test was already performed for the first dataset by Dehon et al. (2017)). Lastly, we performed a LDA on the third dataset considering the subgenera as *a priori* groupings (Suppl. material 4).

Discriminant analyses were performed by using the software R (R Development Core Team 2013). LDA effectiveness was assessed by the percentages of individuals correctly classified to their original taxon (*i.e.*, hit-ratio) in a leave-one-out (LOO) cross-validation procedure based on the posterior probabilities (pp) of assignment. Given the observed scores of an "unknown", the posterior probability equals the probability of the unit to belong to one group compared to all others. The unit is consequently assigned to the group for which the posterior probability is the highest (Huberty and Olejnik 2006). Taxonomic affinities of the Bílina fossil were assessed based on the score in the predictive discriminant space of shapes. Aligned coordinates of the specimens from the three datasets (including the fossil) were used to calculate the same five LDA as discussed above (*vide supra*). We included *a posteriori* the fossil in the five computed LDA space as an "unknown" specimen and calculated its score. Assignment of the fossil was estimated by calculating the Mahalanobis Distance (MD) between "unknown" and the group mean for each taxon (Suppl. materials 5–7). Principal Component Analyses (PCA) were also computed to visualize shape affinities between the fossil and the extant groups in the last dataset (Fig. 7).

Results

Shape variation within the datasets. Analyses based on the first dataset with family, subfamily, and tribe *a priori* groupings are detailed in Dehon et al. (2017), with contemporary families, subfamilies, and tribes well discriminated. Contemporary tribes are also well discriminated in the second dataset (*i.e.*, *Bombus* s.l. and most similar tribes), with a global hit-ratio of 99.6% (Suppl. material 3). Only the extinct tribes Electrapini and Melikertini are not well discriminated, with hit-ratios of 50.0% and 66.7%, respectively. Contemporary subgenera of *Bombus* s.l. are well discriminated in the bumble bee dataset, with a global hit-ratio of 87.4% and 106 misclassified specimens out of 841. Three subgenera show a hit-ratio of 100%: *Alpinobombus* Skorikov, *Kallobombus* Dalla Torre, and *Mendacibombus* Skorikov. Two subgenera have a hit-ratio between 90.0% and 99.0% – *Cullumanobombus* and *Psithyrus* Lepeletier – while two are poorly discriminated in the LDA – *Melanobombus* Dalla Torre and *Orientalibombus* Richards (72.1% and 70.0%, respectively) (Suppl. material 4). Overall, the results show a great reliability for classifying specimens based on the similarity of their forewing shape relative to our reference dataset of forewings. The cross-validation therefore allows us to be confident in the discrimination.

***A posteriori* assignment of the fossil.** The present fossil was assigned to Apidae, to "Non-parasitic Apidae", and to Bombini by using the first dataset (Suppl. materials 5–7). When using the second dataset the fossil was assigned within *Bombus* s.l. (Suppl. material 8), and to subgenus *Cullumanobombus* by the third dataset (Suppl. material 9) (Fig. 7), although it could not discriminate the species as being part of the stem versus crown group. Accordingly, placement of the fossil from the Bílina Mine within *Cullumanobombus* is strongly supported by forewing shape. Continued work including all known fossil Bombini with living relatives will hopefully further refine this placement (Dehon et al. in prep.), particularly in combination with a heuristic phylogenetic exploration of forewing shape (analogous to that of Dehon et al. 2017).

Systematic paleontology

Genus *Bombus* Latreille, 1802
Subgenus *Cullumanobombus* Vogt, 1911

***Bombus* (*Cullumanobombus*) *trophonius* sp. n.**
http://zoobank.org/9FBA6F95-5C97-4F9E-ABC0-EAA8F73403B7
Figs 1–6

Bombus sp. indet.; Prokop and Nel 2003: 166, Dvořák et al. 2010: 36, 78.

Diagnosis. The new species has a wing shape that is consistent with species of the subgenus *Cullumanobombus* (Dehon et al. in prep.). Within this group, the fossil has a wing pattern most similar to *Bombus* (*Cullumanobombus*) *rufocinctus* Cresson, a species distributed widely across the Nearctic (Milliron 1973, Williams et al. 2014), with both species having a similar combination of 3Rs about as long as r-rs but shorter than 4Rs, the basal vein basad 1cu-a, 2Rs arched posteriorly but not as greatly prolonged proximally as in several other species of *Cullumanobombus* (*e.g.*, Milliron 1971), 1m-cu entering second submarginal cell near midpoint (refer to Discussion). The convex pterostigmal border within the marginal cell, less apically narrowed marginal cell, and less arched 2rs-m minimally serve to distinguish the fossil species from *B. rufocinctus*.

Description. ♀: Wings and integument black as preserved (taphonomically altered; coloration and membrane pigmentation as in life unknown) (Figs 1–3); forewing total length 14.6 mm; maximum width 5.10 mm (Figs 2, 4, 5); basal vein (1M) weakly arched at base, comparatively straight along length, basad 1cu-a by about vein width, in line with 1Rs; Rs+M originating anteriorad, 1Rs slightly shorter than r-rs; pterostigma short, slightly longer than wide, border inside marginal cell convex, prestigma nearly as long as pterostigma; marginal cell length 5.1 mm, width 1.1 mm, tapering slightly across its length, free portion of cell slightly shorter than portion bordering submarginal cells, apex rounded and offset from anterior wing margin by

Figure 1. Photograph of holotype of *Bombus* (*Cullumanobombus*) *trophonius*, sp. n., from the Early Miocene of Bílina Mine in northern Bohemia, Czech Republic.

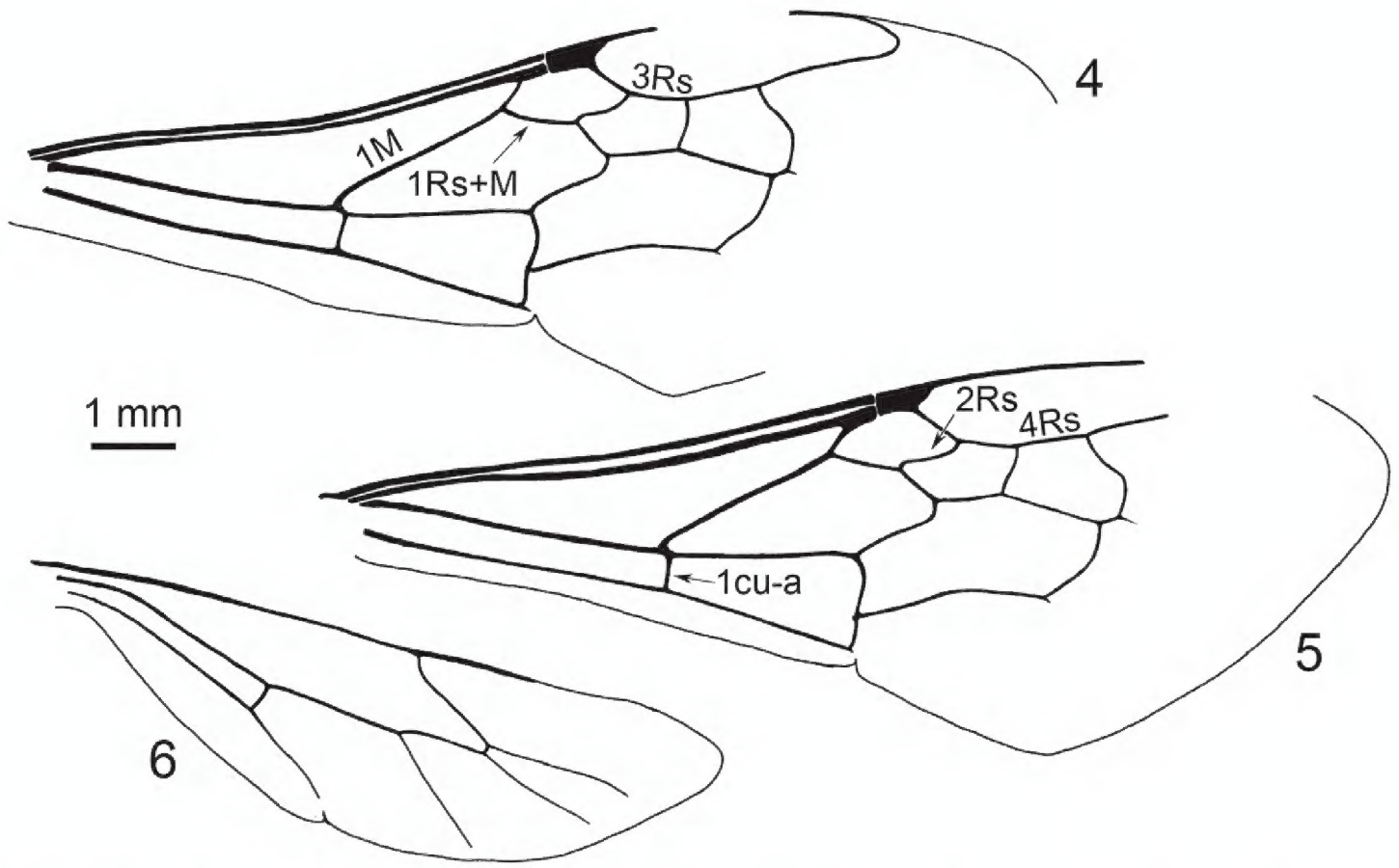
much more than vein width, not appendiculate; 2Rs strongly arched basally and then gently arched outward, giving second submarginal cell distinct proximal extension; r-rs about as long as 3Rs; 4Rs only slightly longer than 3Rs; three submarginal cells of comparatively similar sizes, albeit third slightly larger than first or second; first submarginal cell length 0.9 mm, width 1.0 mm; second submarginal cell length 1.3 mm, width 0.9 mm; third submarginal cell length 1.6 mm, width 1.2 mm; 1rs-m straight, comparatively orthogonal with Rs; 2rs-m arched distally in posterior half; 1m-cu distinctly angulate anteriorly near M, entering second submarginal cell near cell's midlength; 2m-cu weakly and gently arched apically, meeting third submarginal cell at cell's apical

Figures 2–3. Photographs of wings of holotype of *Bombus* (*Cullumanobombus*) *trophonius*, sp. n. **2** Left forewing and right forewing and hind wing **3** Right hind wing.

fifth of length. Hind wing length 9.4 mm, width 2.6 mm (Figs 3, 6). Preserved portion of thorax and legs difficult to discern and interpret, although portion of metatibial corbicula preserved (basal quarter to third), and most sclerites with numerous, long setae.

♂: *Latet*.

Holotype. ♀ (caste uncertain, likely a worker), ZD0003, Early Miocene, Most Formation, Clayey Superseam Horizon, Holešice Member (No. 30), Bílina Mine near Bílina, Czech Republic; deposited in the museum collection of the Bílina Mine Enterprises, Bílina, Czech Republic.



Figures 4–6. Line drawings of wing venation of holotype of *Bombus* (*Cullumanobombus*) *trophonius*, sp. n., as preserved. **4** Left forewing **5** Right forewing **6** Right hind wing.

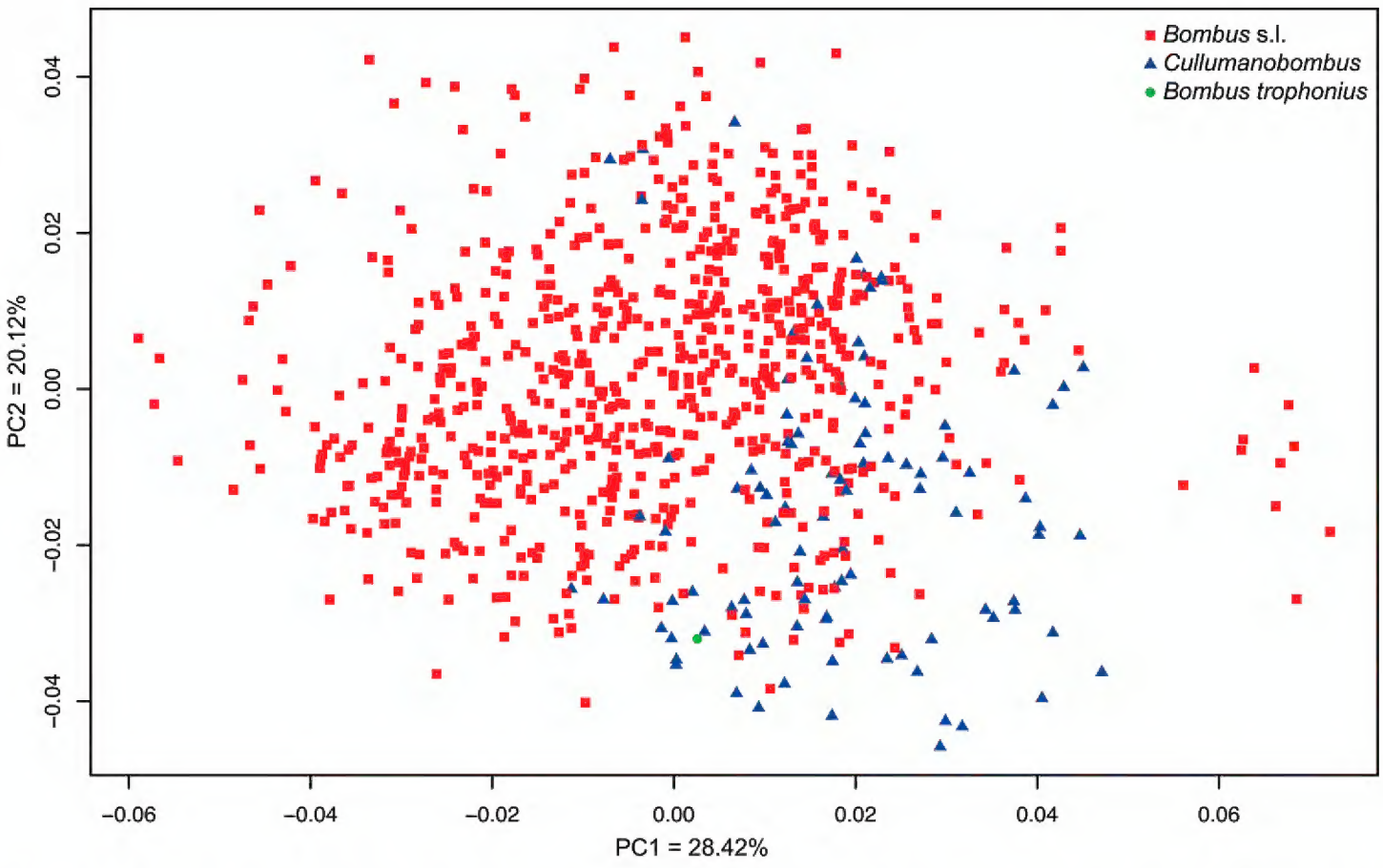


Figure 7. Ordination of the fossil along the two axes of the PCA (PC1 = 28.42% and PC2 = 20.12%) in the *Bombus* s.l. dataset, with extant specimens of *Cullumanobombus* highlighted in blue.

Etymology. The specific epithet is taken from the Greek mythological hero, Trophonius, one of the two brothers who absconded with the treasure of King Hyrieus and who fled into caverns at Lebadaea (today's Livadeia in Boeotia). Trophonius is generally associated with bees and the underworld since, according to legend, it was a swarm of bees that led a boy to rediscover his cave, bringing his spirit honor and peace.

Discussion

Naturally, it is challenging in the absence of clear characters from the head, mandibles, genitalia, or patterns of coloration to make a globally satisfactory assessment of the present fossil. Nonetheless, a morphometric shape analysis of the fossil among other living and fossil bombines confidently placed *B. trophonius* within the subgenus *Cullumanobombus*, in the broad sense as advocated by Williams et al. (2008). Most species of *Cullumanobombus* have New World distributions, except for *B. cullumanus* (Kirby), *B. semenoviellus* Skorikov, *B. unicus* Morawitz, and *B. vogti* Friese which are found in the Old World (Milliron 1973, Williams 1985). The overall combination of wing traits tends to exclude *B. trophonius* from all groups within *Cullumanobombus* with the exception of one. For example, in most species of the *robustus*, *fraternus*, *griseocollis*, *cullumanus*, *rubicundus*, and *brachycephalus* species groups 3Rs is longer than r-rs (rather than about as long as r-rs in *B. trophonius*), and in some, such as the latter two groups, it is also longer than 4Rs (rather than 4Rs longer than 3Rs as is the case in *B. trophonius*). In addition, in several groups 1m-cu enters the second submarginal cell basal its midpoint (*e.g.*, *brachycephalus* and *fraternus* groups), rather than near the midpoint in *B. trophonius*. The second submarginal cell is frequently more pronouncedly elongate proximally, owing to a more dramatically arched 2Rs, in many species of the *rubicundus* and *robustus* groups, while 2rs-m is less arched in the *brachycephalus*, *robustus*, *fraternus*, and *griseocollis* groups and the basal vein and 1cu-a are usually confluent in *B.* (*C.*) *brachycephalus* Handlirsch. The only species within the clade that has the same combination of features as are present in the fossil is *B.* (*C.*) *rufocinctus*. The latter species is common from North Amercia to Mexico. Interestingly, *B. rufocinctus* is considered basal within *Cullumanobombus* (Cameron et al. 2007, Hines 2008), and the overall shared pattern between their wings may be symplesiomorphies (based on the plesiomorphic placement of *B. rufocinctus* and its wing venation relative to more derived species of *Cullumanobombus*), which would be intuitively pleasing if *B. trophonius* were representative of a stem group to the subgenus. In *B. rufocinctus* the marginal cell is often more narrowed apically than in *B. trophonius*, and the former has worker forewing lengths shorter than in the fossil (approximately 11 mm in *B. rufocinctus*, versus over 14 mm in *B. trophonius*). However, queens of *B. rufocinctus* can easily exceed 14 mm in forewing length, and if the holotype of *B. trophonius* was a queen, then the two would be of approximately similar proportions. The age of *B. trophonius* is in general accordance with what one might except of a stem-group *Cullumanobombus* based on the divergence time estimations of Hines (2008). The palaeoclimate of the Bílina

locality was subtropical/warm temperate and temperate (Kvaček et al. 2004), while extant species of *Cullumanobombus* exploit a wide variety of climatic niches, mainly dry and warm, but not boreal. While there remains a plethora of questions regarding the complete characterization of *B. trophonius*, the species apparently represents an important record for *Cullumanobombus* and the discovery of more complete material in the future will undoubtedly continue to bring revelations regarding bumble bee evolution and biogeography during the Neogene.

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Supplementary material 1

Table S1

Authors: Jakub Prokop, Manuel Dehon, Denis Michez, Michael S. Engel

Data type: Microsoft Word Document (.docx)

Explanation note: First dataset for geometric morphometric analyses encompassing 988 specimens from 234 species, 141 genera, 53 tribes, 18 subfamilies, and seven families of Anthophila (Apoidea). All included groups have three submarginal cells. N1= number of species; N2 = number of specimens.

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Link: https://doi.org/10.3897/zookeys.710.14714.suppl1

Supplementary material 2

Table S2

Authors: Jakub Prokop, Manuel Dehon, Denis Michez, Michael S. Engel

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Second dataset for the geometric morphometric analyses. This sample includes 872 specimens from 247 species, 14 genera, and six tribes of Apidae. N = number of specimens.

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Link: https://doi.org/10.3897/zookeys.710.14714.suppl2

Supplementary material 3

Table S3

Authors: Jakub Prokop, Manuel Dehon, Denis Michez, Michael S. Engel

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Specimen assignment in tribes using the cross-validation procedure in the LDA of forewing shape in the "*Bombus* s.l. + comparison groups" dataset. Original groups are along the rows, predicted groups are along the columns. The hit ratio (HR%) is given for each tribe.

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Link: https://doi.org/10.3897/zookeys.710.14714.suppl3

Supplementary material 4

Table S4

Authors: Jakub Prokop, Manuel Dehon, Denis Michez, Michael S. Engel

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Specimen assignment in subgenera using the cross-validation procedure in the LDA of forewing shape in the dataset of *Bombus* s.l. Original groups are along the rows, predicted groups are along the columns. The hit ratio (HR%) is given for each subgenus.

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Link: https://doi.org/10.3897/zookeys.710.14714.suppl4

Supplementary material 5

Table S5

Authors: Jakub Prokop, Manuel Dehon, Denis Michez, Michael S. Engel

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Mahalanobis distances (MD) between familial centroids and the 979 specimens, and the fossils and familial centroids in the tribal dataset.

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Link: https://doi.org/10.3897/zookeys.710.14714.suppl5

Supplementary material 6

Table S6

Authors: Jakub Prokop, Manuel Dehon, Denis Michez, Michael S. Engel

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Mahalanobis distances (MD) between subfamilial centroids and the 979 specimens, and the fossils and subfamilial centroids in the tribal dataset.

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Link: https://doi.org/10.3897/zookeys.710.14714.suppl6

Supplementary material 7

Table S7

Authors: Jakub Prokop, Manuel Dehon, Denis Michez, Michael S. Engel

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Mahalanobis distances (MD) between tribal centroids and the 979 specimens, and the fossils and tribal centroids in the tribal dataset.

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Link: https://doi.org/10.3897/zookeys.710.14714.suppl7

Supplementary material 8

Table S8

Authors: Jakub Prokop, Manuel Dehon, Denis Michez, Michael S. Engel

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Mahalanobis distances (MD) between tribal centroids and the 975 specimens, and the fossils and tribal centroids in the "*Bombus* s.l. + comparison groups" dataset.

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Link: https://doi.org/10.3897/zookeys.710.14714.suppl8

Supplementary material 9

Table S9

Authors: Jakub Prokop, Manuel Dehon, Denis Michez, Michael S. Engel

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Mahalanobis distances (MD) between subgeneric centroids and the 841 specimens, and the fossils and subgeneric centroids in the *Bombus* s.l. dataset.

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Link: https://doi.org/10.3897/zookeys.710.14714.suppl9